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Bilateral jaw elements in *Amiskwia sagittiformis* bridge the morphological gap between gnathiferans and chaetognaths

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Summary

Amiskwia sagittiformis Walcott 1911 is an iconic soft bodied taxon from the Burgess Shale [1-3]. Originally interpreted as a chaetognath [1], but later interpreted as a pelagic nemertean [2], or considered of uncertain affinity [3]. Part of this ambiguity is due to direct comparisons with members of the crown groups of extant phyla [4] and a lack of clarity regarding the systematic position of chaetognaths, which would allow for assessing character polarity in the phylum with respect to outgroups. Here we show that *Amiskwia* preserves a bilaterally arranged set of head structures visible in relief and high reflectivity. These structures are best interpreted as jaws situated within an expanded pharyngeal complex. Morphological studies have highlighted likely homology between bilateral and chitinous jaw elements in gnathiferans and chaetognaths [5], which is congruent with a shared unique HOX gene that suggest a close relationship between Gnathifera and Chaetognatha [6]. Molecular phylogenetic studies have recently found gnathiferans to be a deep branch of Spiralia and Chaetognaths either a sister group to Spiralia [7] or forming a clade with gnathiferans [6, 8]. Our phylogenetic analyses renders

Gnathifera paraphyletic with respect to Chaetognatha and we therefore suggest that *Amiskwia* is best interpreted as a stem chaetognath, but crown gnathiferan.

Keywords: Chaetognatha; Burgess Shale; Cambrian Explosion; Gnathifera; Spiralia; Lophotrochozoa

Results

Several early Palaeozoic taxa have evaded placement in animal phylogeny and remain enigmatic. *Amiskwia saggitiformis* (Figure 1) is such an example, possessing an apparently chimeric suite of characters that obscure its phylogenetic affinities. *Amiskwia* is a rare taxon in the Burgess Shale. Putative specimens of the same genus are known from the early Cambrian of Chengjiang [9]. *Amiskwia* possesses a distinct anterior region, separated from a slender trunk with a single pair of lateral fins and distinct horizontal tail (caudal) fin. This is reminiscent of nektonic spiralian, such as chaetognaths [1] and pelagic nemerteans [2] to which it has been previously assigned. In addition, *Amiskwia* carries two prominent head tentacles (Figure 1,2).

Conway Morris [3] reassessed the morphology of *Amiskwia*, and found key apomorphies for both proposed assignments to be lacking. The gut of *Amiskwia* terminates immediately before the tail fin, and so the trunk-tail septum that characterises extant chaetognaths is apparently absent, as are fin rays. Typical chaetognaths also possess an anterior and posterior pair of lateral fins, although a single pair is present in some genera, such as *Eukrohnia* and the benthic genus *Spadella* [10-12]. Butterfield [13] noted possible similarities between *Amiskwia* and chaetognaths in their cuticle and their likely preservation potential in Burgess Shale type (BST) Lagerstätten.

Conway Morris [3] discussed the presence of two reflective patches, previously interpreted as paired cerebral ganglia [14]. While accepting these structures as nervous tissue [3], he rejected the notion that they resemble the condition observed in pelagic nemerteans. In addition, the absence of anterior testes and rhyncocoel prompted Conway Morris to interpret *Amiskwia* as a member of an independently evolved pelagic lineage with similarities to extant phyla arising due to convergence [3].

We reassess the nature of this pair of reflective patches and suggest that given their preservation, morphology and location in the body that they are best interpreted as a pair of pharyngeal jaws, that are similar to those of gnathiferans. Together with a number of previously highlighted similarities between gnathiferans and chaetognaths in their overall morphology we argue that *Amiskwia* shares characters with both groups, supporting emerging evidence for a shared ancestry.

Jaws in *A. sagittiformis*

The paired anterior structures have been identified primarily through their high reflectivity [3]. However, when the specimens are coated with ammonium chloride and imaged with low angle illumination, they exhibit distinct relief with demarcated margins (Figure 1A,D). The two structures are situated in association with a central reflective structure with little relief (Figure 1A,C), which transcends the median of the trunk as a narrow and well-delineated line from the posteriormost part of the trunk behind the posterior tail fin. This median reflective structure expands to encompass the paired head structures (Figure 1C).

The prominent relief exhibited by these paired structures is indicative of decay resistance, such as in tissues originally hardened through sclerotization or mineralisation, rather than nervous tissue [3, 14, 15]. While nervous tissues have now been positively confirmed in BST panarthropods [16-18], their preservation is less distinct and they do not exhibit distinct relief, as illustrated in *Kerygmachela* [19] and *Waptia* [15]. The median reflective structure with no relief (Figure 1B) has been interpreted as the alimentary tract [3]. We therefore propose that the association of the paired anterior structures with the alimentary tract in the head identifies them as feeding structures: a bilaterally paired jaw apparatus situated within an enlarged pharyngeal cavity. In USNM 198670, the structures exhibit a subtriangular shape, while in two larger specimens (USNM 57644, 57645) the structures are more kidney-shaped (Figures 1F-H). These two specimens split along the dorsal integumentary surface. Imaging with crossed polarised light reveals that the kidney shaped structure is a thinner membrane surrounding the smaller and more sclerotised (evident from its darker colour and relief) jaw element (Fig 1F). It appears as if the jaw in *Amiskwia* is a single paired set of elements, although it is difficult to eliminate that it is composed of several adjoining elements that are conflated by compaction and preservation.

General anatomy of *Amiskwia*

The head of *Amiskwia* is demarcated from the trunk by a structure preserved with both reflectivity and slight relief (Fig 2A-C, F-H, I-K), suggesting the presence of a cuticularized hood. There is a set of lateral fins and a tail fin that both have a distinct boundary with the body. Fin rays have not been described in *Amiskwia*, but we note the presence of lineations possibly consistent with fin rays in UMNH 57644 (Figure 2L,M).

The median reflective structure conforms in trajectory, appearance and preservation to an alimentary tract. It is a straight tube that expands anteriorly to contain the jaw apparatus terminating subterminally in front of the horizontal tail fin. USNM 57645 and USNM 198670 preserve a fine integumentary boundary anterior to the jaw apparatus and there is a tubular infill of the gut posterior to it, which may be the location of the mouth opening (Figure 1E), which is presumably ventral. We note that the specimen referred to the fossil chaetognath *Protosagitta* by Shu et al. [20], ELI-EJ-0009, appears to be another occurrence of *Amiskwia* with an internal jaw apparatus, preserving anterior antennae as well as fin rays.

Shared characters of gnathiferans , chaetognaths and *Amiskwia*

Gnathifera is a clade composed of Rotifera, Micrognathozoa and Gnathostomulida [21, 22] that is united by the shared presence of bilaterally symmetrical jaw apparatus made of chitin that have a distinctive microstructure [21]. Nielsen [5] proposed an expanded Gnathifera, which also included chaetognaths, proposing a homology of the chaetognath grasping spines, anterior and posterior teeth and gnathiferan jaws, but subsequently abandoned this hypothesis [23]. Both the jaws in chaetognaths and gnathiferan taxa are composed of chitin, which may preserve in fossils, demonstrated by mollusc radulae and chaetae in BST taxa [24, 25]. The jaws of other lophotrochozoans, such as annelids, are typically sclerotized proteins that are hardened by other materials, such as transition metals and melanin [26, 27], although the molluscan radula and cephalopod beaks are also composed of chitin [28, 29].

The hypothesis of a relationship between chaetognaths and gnathiferans received a recent revival with the discovery of a shared Hox 6 gene duplication (Med-Post) in rotifers and chaetognaths [6]. Consequently, the authors [6] noted putative morphological synapomorphies shared by chaetognaths and gnathiferans, with chaetognaths sharing more

characters with rotifers than the other gnathiferan phyla (gnathostomulids and micrognathozoans). Characters shared by rotifers and chaetognaths include a tripartite body, absence of locomotory trunk cilia and an anus terminating medio-posteriorly in a dorsal position rather than in a ventral position (which is observed in many lophotrochozoans and gastrotrichs). Both taxa also have coronal ciliary bands that are either multiciliate (rotifers) or monociliate (chaetognaths) [6]. Further similarities are observed in the nervous system, including innervation of the feeding apparatus, lateral antennae and the corone [6]. Furthermore, Hox 4 is expressed in the ventral ganglion in chaetognaths and the caudal ganglion of rotifers, suggesting homology. Early cleavage departs from the general spiral cleavage widespread in lophotrochozoans/spiralian by having early D-quadrant cleavage without formation of 4d mesentoblast. Finally, the pharyngeal jaw apparatus and chitinous membranes within the mastax of gnathiferans was proposed as homologous to the grasping spines/jaw apparatus of chaetognaths [6], which has also been discussed by other authors [20, 30].

While developmental characters and hox genes cannot be gleaned from fossils, general anatomical features may be surmised. In *Amiskwia* the body does not display a clearly tripartite body plan, as in rotifers and chaetognaths, but the anus is subterminal given the presence of a tail fin posteriorly to the termination of the preserved digestive tract. Furthermore, the head is differentiated from the mid-body, which is likewise observed in chaetognaths and some gnathiferans, such as gnathostomulida.

The paired anterior structures of *Amiskwia* resemble the pharyngeal jaw apparatus in gnathiferans in being laterally paired, in a position posterior to the mouth opening within the head. However, the gnathiferan jaw possesses multiple elements, which vary in form and number of elements amongst the different phyla (Rotifera, Micrognathozoa and Gnathostomulida) [29]. Untangling the precise homology of internalised jaw apparatuses, grasping spines and anterior and posterior teeth [31, 32] will require further scrutiny and is potentially complicated by serial homology. For example in acanthocephalans, which have been shown to be parasitic rotifers based on sperm ultrastructure and molecular phylogenetics [33, 34], the mastax is modified into an eversible proboscis with many teeth arranged in a quincunx pattern that cannot be easily compared to any particular gnathiferan jaw element in Rotifera or other taxa.

Chaetognaths are among the oldest bilaterian fossils that are easily identified as members of extant phyla, with a small carbonaceous fossil record from the Terreneuvian as well as protoconodonts representing the grasping spines of chaetognaths [35, 36]. *Oesia disjuncta* has previously been interpreted as a chaetognath [37], but this taxon is now recognised as a hemichordate [38, 39]. Unequivocal fossil chaetognaths from the Burgess Shale (*Capinatator*) [40] and Chengjiang (*Ankalodous*) [20] have recently been shown to possess up to four clusters of self-similar grasping spines, but lack anterior/posterior teeth [20, 40], although teeth may be present in *Protosagitta* from Chengjiang [36]. It might therefore be possible that the anterior/posterior teeth are modified serial homolog clusters of an original set of grasping spines and that all the chitinous elements in chaetognaths are modified from elements with a plesiomorphic grasping spine like morphology. In *Capinatator*, the grasping spines are similarly preserved with high reflectivity like the jaws of *Amiskwia* [40].

Characters shared by *Amiskwia* and chaetognaths

Although the jaw apparatus of *Amiskwia* appears similar to the gnathiferan condition in both morphology and topological relationship to the mouth and digestive tract, there are a number of distinct similarities between chaetognaths and *Amiskwia*, such as the present of lateral fins and a horizontal caudal fin [41]. While most chaetognaths possess two pairs of lateral fins, the phragmophore chaetognaths (e.g. spadelliids, eukrohniids and heterokrohniids) as well as the krohniids have only one lateral fin [42]. Chaetognaths possess collagenous fin rays [43], which are not clearly visible in *Amiskwia* from the Burgess Shale, except putatively in one specimen where faint striations are visible (Figure 2L,M). Fin rays, or even well preserved fins have not been described from any Burgess Shale, or Chengjiang chaetognath [36, 40], except for the putative amiskwiid described as a chaetognath recently [20]. The lack of commonly preserved fin rays is perhaps not surprising, given the generally poor, to non-existent, preservation potential of proteinaceous tissues [44, 45].

In extant chaetognaths the body lacks a thick cuticle, except for the cephalic hood [46], which appears to be present in *Amiskwia* where it is visible as a distinct arcuate margin that defines the head and transects the head trunk division (Figure 2A-C, F-K). The presence

of a hood in the Burgess Shale chaetognath *Capinatator* [40] may explain the enhanced preservation of the head relative to the body in these specimens.

The presence of only a subset of chaetognath synapomorphies in *Amiskwia* (Table S1) suggests a phylogenetic position outside of the chaetognath crown group. This includes the lack of a trunk tail septum proximal to the subterminal anus and the chitinous feeding elements being situated inside a mastax-like lumen. In chaetognaths, the jaw apparatus forms a ventral surface with the three distinct clusters of elements (grasping spines, anterior and posterior teeth) surrounding the mouth opening. The whole complex is held within the retractable cephalic hood.

Tentacles are present in spadellid chaetognaths and abdelloid rotifers [6, 47]. These are placed on the posterior margin of the head or dorsally, while in *Amiskwia* they are placed at the anteriormost margin. Homology of these structures may therefore be equivocal based on the criterion of conjunction [48] but the head in chaetognaths may have undergone some degree of eversion to allow the jaw apparatus to become externalised in a ventral position. Such eversion would displace features on the head posteriorly.

Inquicus fellatus

The presence of chaetognaths and a diversity of spiralian phyla by the early Cambrian clearly demonstrates that the stem lineage of Gnathifera must have existed by this time period, based on phylogenetic constraints. *Inquicus fellatus* is a recently described and similarly enigmatic taxon that is known from the early Cambrian of South China. This taxon is found attached to other organisms (*Cricocosmia* and *Mafangscplex*) via a posterior attachment structure [49] and shares several similarities with *Amiskwia* and gnathiferans, including a subterminal anus, a differentiated head and neck region and a prominent relief structure at the anterior contained in the digestive tract [49]. The preservation of this structure suggests decay resistance and its association with the anterior-most portion of the alimentary canal is similar to the jaw condition observed in gnathiferans. The presence of a posterior attachment structure is shared with both rotifers and micrognathozoans, although such attachment structures are widespread among spiralians with small body size, such as gastrotrichs [50]. The absence of a corona [49] may be a consequence of small size and the limitations of preservation.

Phylogenetic analysis

In order to assess the likely affinity of *Amiskwia* among spiralian we conducted a Bayesian phylogenetic analysis of 140 characters and 33 taxa (Figure 3, Figures S2,3). Our dataset was expanded from a previous matrix focused on metazoan relationships [51]. We resolve *Amiskwia* as the earliest diverging branch in the chaetognath stem group. Total group chaetognaths are recovered as the sister group of Rotifera. We also included *Inquicus fellatus* [16], which resolves as a crown gnathiferan, as a sister to Rotifera plus Chaetognatha. The fossil chaetognaths with supernumerary grasping spines from the Cambrian are recovered in the chaetognath stem group, whereas *Protosagitta* [36] is in a polytomy with crown group chaetognaths (Figure 3).

Discussion

Assigning *Amiskwia* to chaetognaths has long been considered problematic due to their lack of the canonical grasping spines. With the introduction of stem and crown group thinking [52] it has been recognised that stem lineages only possess a subset of the defining characteristics of the crown group, and can exhibit unique synapomorphies. Fossils are now considered in a more holistic context, by analysing them in their appropriate taphonomic [45], and improved phylogenetic context through both morphology [53] and molecular phylogenetics [54].

Our findings suggest that *Amiskwia* is an important stem lineage with a unique combination of characters shared by both gnathiferans and chaetognaths. Molecular phylogenies have resolved chaetognaths as the sister group of Spiralia [8, 55, 56], within Ecdysozoa [57, 58] or sister to/within protostomes [59-61]. A subset of phylogenomic analyses have recovered chaetognaths as a clade with gnathiferans [8, 62]. Phylogenetic analyses focusing on chaetognath relationships suggest that ‘Phragmophora’ is paraphyletic with respect to Apharesiphora, and that the presence of a single pair of fins is plesiomorphic [42], which is congruent with a single pair of fins in the stem chaetognath *Amiskwia*.

Our phylogenetic analyses recover *Amiskwia* as a stem chaetognath and chaetognaths and rotifers are resolved as sister taxa, rendering the typically recognised Gnathifera [63] paraphyletic. Although the shared possession of the MedPost hox gene duplication in rotifers and chaetognaths could support this hypothesis further, no studies of

the hox gene complement of the other gnathiferan groups has been undertaken. Therefore, it is also possible that chaetognaths are the sister group of the other gnathiferans (Figure 4b) and that characters shared by chaetognaths and rotifers have been reduced or lost in the other phyla. One phylogenomic study obtained this result among other alternatives, resolving chaetognaths in a more traditional position as the sister group of Spiralia [8] and an older study recovered monophyly of a rotifer-chaetognath clade [62]. In our analyses, monophyly of a rotifer-chaetognath clade is independent of the inclusion of *Amiskwia* (Figure S2). Analyses constraining the monophyly of a rotifer, gnathostomulid, micrognathozoan clade (Figure S3A) or constraining chaetognaths as the spiralian sister lineage (Figure S3B) consistently recover *Amiskwia* as a stem group chaetognath.

It is possible that micrognathozoans and gnathostomulids are independently secondarily miniaturised [64] (Figure 4b) and have lost synapomorphies in a chimaeric fashion that cannot be detected by our phylogenetic methods. Ultimately, the relationship among gnathiferans and chaetognaths are in need of further scrutiny through phylogenomic studies and a more complete picture of their genomic complexity, such as shared gene duplications and losses [6]. Likewise, the discovery of additional fossil taxa may reveal that some characters that are present only in extant chaetognaths had a broader distribution in the past, which may refine the phylogenetic position of *Amiskwia*.

Conclusions

Fröbius and Funch [6] argued for a relationship between chaetognaths and rotifers within Gnathifera based on a shared hox gene duplication (MedPost). A series of morphological and developmental similarities between these two clades were also presented. They noted that while one line of evidence alone may be weak, the combination of several “*provide an informative basis for this relationship*”. We can now present palaeontological data that further corroborate this hypothesis. Chaetognaths may be the sister group of, or nested within, the Gnathifera. Clarifying the precise relationship among these taxa and discovery of additional fossil taxa may resolve outstanding questions in spiralian evolution such as if gnathiferans evolved from a macroscopic ancestor, or whether chaetognaths and spirilians as a whole evolved from microscopic ancestors [64].

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Author contributions. JV and LP photographed the specimens at the Smithsonian Institution on two consecutive visits. JV first noted the presence of jaws in *A. sagittiformis*. LP assembled the character matrix and conducted the phylogenetic analysis. JV and LP made drawings and figures. Both authors contributed to the interpretation of the fossils and writing of the manuscript.

Declaration of interests. We declare no competing interests.

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Figure Captions

Figure 1 Bilateral jaw apparatus in *Amiskwia sagittiformis*. (A-E) USNM 198670 and (E-F) USNM 57645. (A) Photographed in low angle lighting, coated with ammonium chloride sublimate. (B) Submerged in water under high angle illumination. (C) Interpretative drawing, outlining the jaw apparatus (pink) in relation to the digestive tract (grey), abbreviations: Tentacle—Te; Jaw—Ja; Cephalic Hood—Ch; Lateral Fin—Lf; Gut/digestive tract—Gu; Anus—An; Tail/caudal fin—Tf. (D) Close up of head with high angle illumination and submerged in water. Jaw apparatus is the highly reflective paired structures. (E) same view as in D, when imaged with ammonium chloride sublimate and low angle illumination. Jaw apparatus is preserved with distinct relief. (F) USNM 57645 imaged with polarised light. (G) photographed under high angle illumination submerged in water (H) Interpretative drawing of indicating sclerotised jaw apparatus (pink) in relation to the gut (grey). Abbreviations: Tentacles—Te; Jaw—Ja; Jaw membrane—Jm; Cephalic hood—Ch; Digestive tract/gut—Gu. See also Figure S1.

Figure 2 The cephalic hood, sub terminal anus and tail fin of *Amiskwia sagittiformis* (A-E) USNM 198670. (A) Detail of head in low angle illumination, coated with ammonium chloride sublimation, (B) Imaged in high angle illumination submerged in water. (C) Interpretative drawing indicating margin of cephalic hood (Ch, brown). (D) Close up of posterior trunk section. (E) interpretative drawing of area shown in D, indicating gut trajectory (grey)

terminating subterminally. (F - H) USNM 57644. (F) Closeup of head in low angle illumination and coated with ammonium chloride sublimation. (G) Closeup of head illuminated with high angle illumination and submerged in water. (H) interpretative drawing, indicating outline of cephalic hood (Ch, brown). (I-K) USNM 57645. (I) imaged with crossed polarised light. (J) Imaged with high angle illumination, submerged in water. (K) interpretative drawing indicating margin of the cephalic hood. (L,M) USNM 57644. (L) closeup of tail imaged with high angle illumination, submerged in water. (M) Interpretative drawing of area shown in (L) indicating putative fin rays (Fr), inferred position of anus (An) based on digestive tract trajectory. See also Figure S1.

Figure 3 Bayesian phylogeny of protostomes consisting of 33 taxa and 140 characters incorporating *Amiskwia*, *Inquicus* and fossil chaetognaths from the Cambrian. Phylogeny inferred under the mk + gamma model, numbers at nodes are posterior probabilities. Thumbnails at bottom of figure show reconstructions of relevant extant and extinct gnathiferan and chaetognath taxa. See also Methods S1 and Figures S2, S3 and Table S1.

Figure 4 Alternative evolutionary scenarios and character evolution. (A) topology based on our phylogenetic analysis, recovering monophyly of Gnathifera sensu Nielsen (2001) [5] but with chaetognaths as a sister taxon to Rotifera. (B) Alternative topology with chaetognaths as a sister taxon to all other gnathiferans, based on an alternative analysis where Gnathostomulida, Rotifera and Micrognathozoa are constrained to be monophyletic with respect to Chaetognatha, full results of this analysis are shown in Figure S3B. See also Methods S1 and Figures S2, S3 and Table S1.

STAR methods

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact Jakob Vinther (Jakob.vinther@bristol.ac.uk)

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The fossil specimens of *Amiskwia saggitiformis* are from the Walcott Quarry locality of the middle Cambrian Burgess Shale and are housed at the National Museum of Natural History, Washington D.C. (USNM). The specimen of *Inquicus felatus* (YKLP 13235a) are from the Ercaicun section, Haikou, Yunnan, China and are housed at the Yunnan Key Laboratory for Palaeobiology (YKLP).

METHOD DETAILS

Fossil preparation and photography

Images of the *Amiskwia* material were taken with a Nikon D90, using a 60 mm nikkor macro lens and a Canon EOS 5D camera with Canon MP-E 65 mm (1-5X) or Canon EF 100 mm macro lenses. Photographs were taken using a variety of lighting conditions, including at high angle, underwater and with cross polarised light. Images taken with low angle lighting used Magnesium Chloride to enhance contrast.

Interpretative drawings

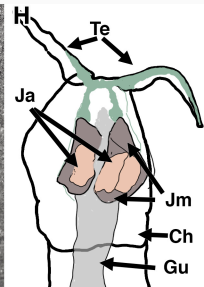
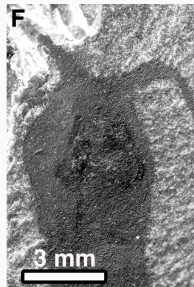
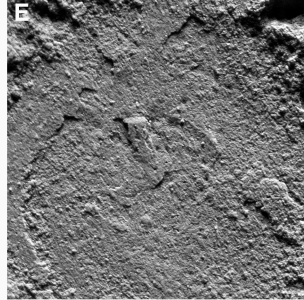
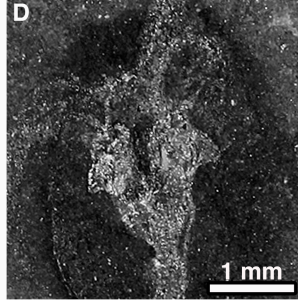
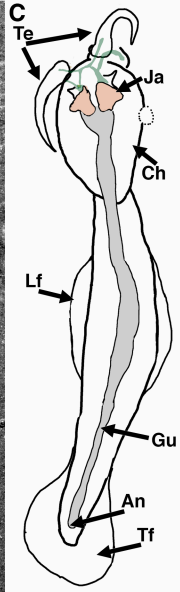
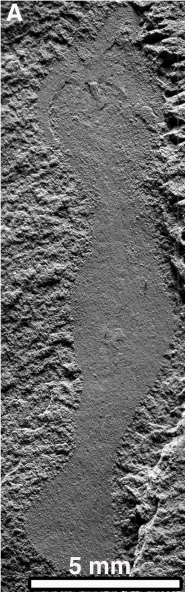
Interpretative drawings were made by tracing fossil specimens photographed using different lighting conditions in Adobe Photoshop.

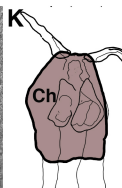
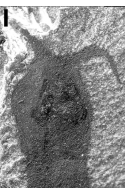
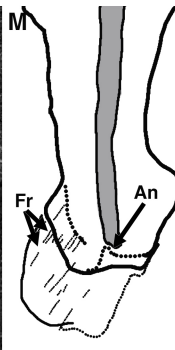
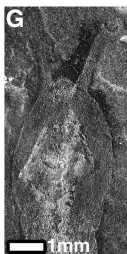
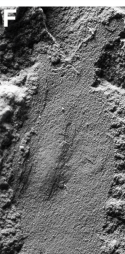
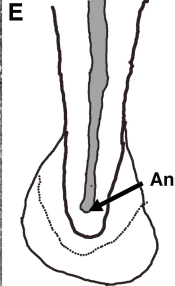
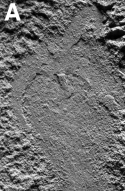
QUANTIFICATION AND STATISTICAL ANALYSIS

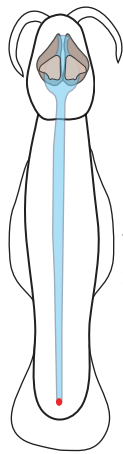
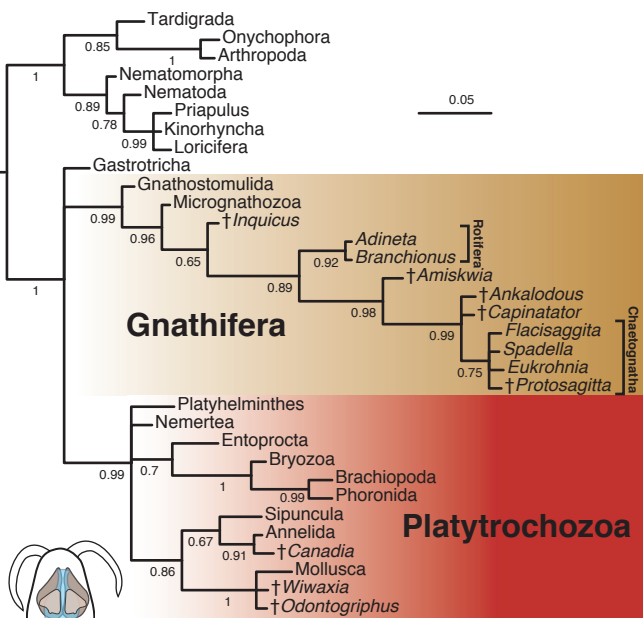
Phylogenetic analyses

Phylogenetic analysis was carried out using the mkv model [65] in MrBayes 3.2.6 [66]. The matrix consist of 33 taxa and 140 characters. As our analysis incorporated autapomorphies and constant characters, we did not employ a correction for the ascertainment bias. Analyses converged rapidly and ran for 5000000 generations with the first 10% of samples discarded as burn in. Convergence was assessed using ESS scores ($>>200$), the average deviation of split frequencies (<0.01) and PSRF values ($=1.00$) in MrBayes. Tree samples were summarised as a majority rule consensus. Additional analyses used identical numbers of generations and burn in but employed backbone topological constraints that constrained the phylogenetic position of chaetognaths relative to the other spiralian phyla. See also Methods S1.

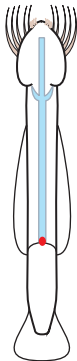
Methods S1 – Details of phylogenetic analysis and character matrix. Related to Figures 3 and 4.







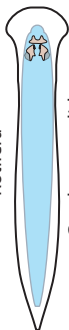
†*Amiskwia*



Chaetognath



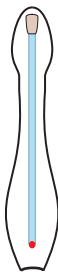
Rotifera



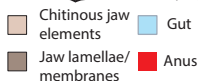
Gnathostomulida

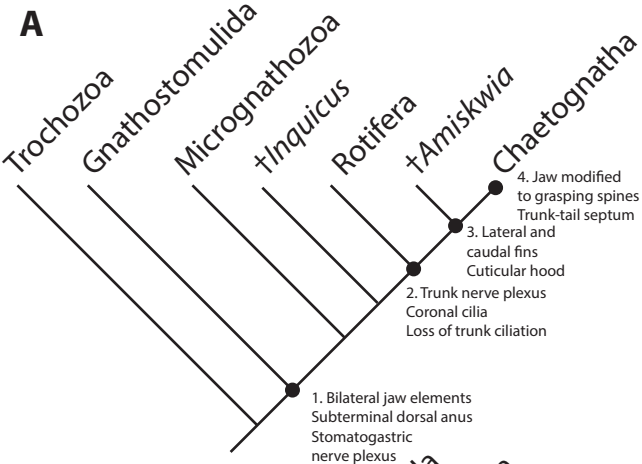
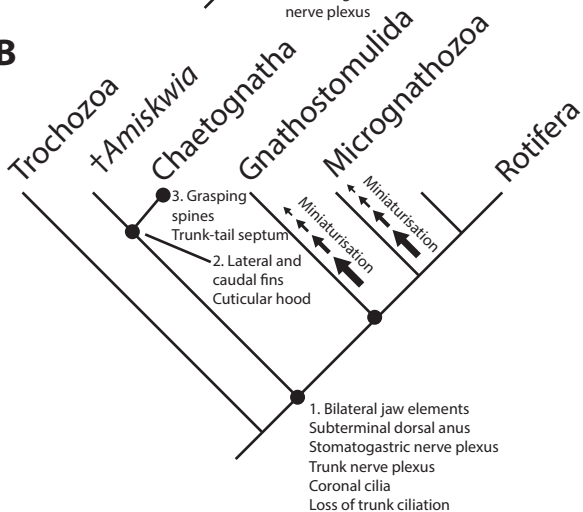


Micrognathozoa



†*Inquicus*



A**B**

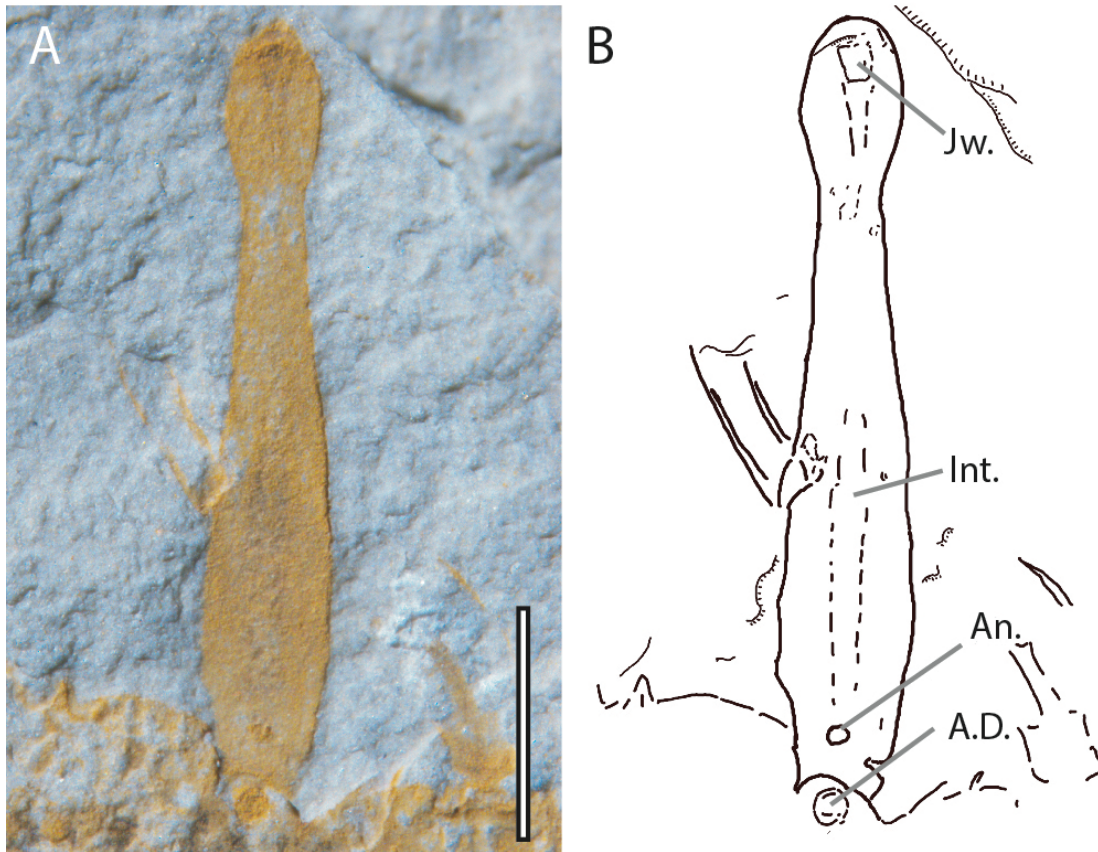


Figure S1 Morphology of *Inquicus felatus* from the early Cambrian Chengjiang biota of South China. Related to Figures 3 and 4. (A,B) holotype YKLP 13226a. (A) specimen photo courtesy of Peiyun Cong, (B) interpretive drawing. Scale bar 1mm. Jw. – jaw, Int. – intestine, An. –anus, A.D. – attachment disc.

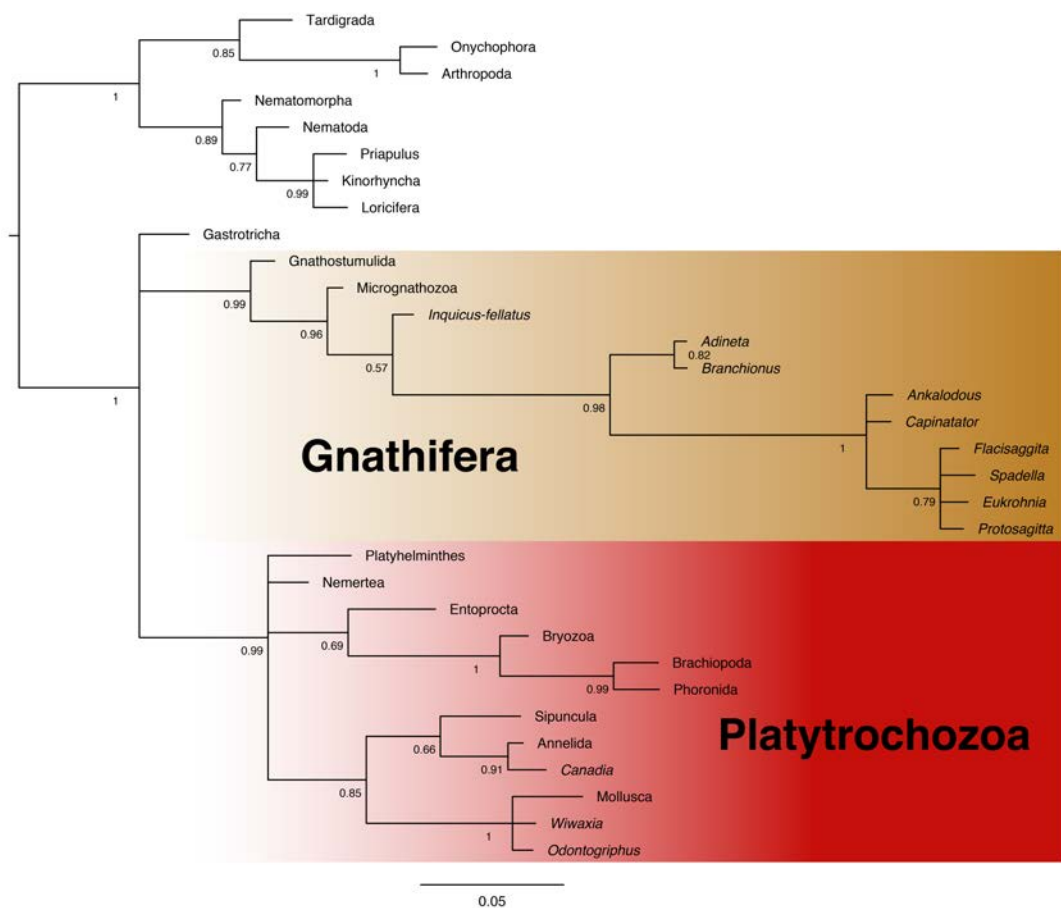


Figure S2 Additional phylogenetic results. Related to Figure 3 and Figure 4. Morphological phylogeny of spiralian with Ecdysozoa as an outgroup with *Amiskwia* omitted from the dataset. Phylogeny inferred under the mk + gamma model in MrBayes.

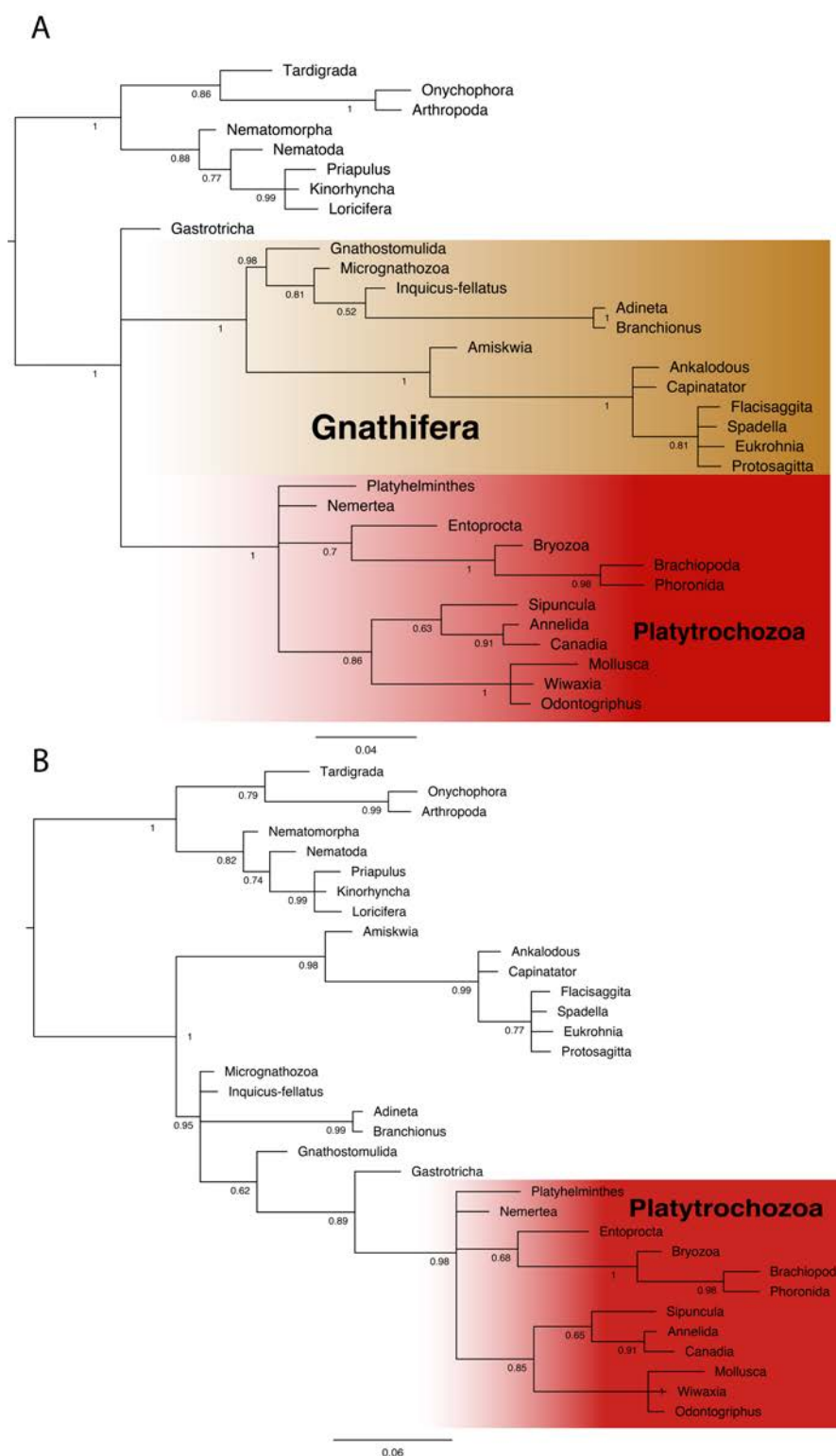


Figure S3. Alternative topologies inferred using different topological constraints. Related to Figure 3 and Figure 4. (A) Morphological phylogeny of spiralian outgroups with Ecdysozoa as an outgroup with a soft topological constraint that forces the monophyly of a Gnathostomulida,

Rotifera, Micrognathozoa clade. (B) Morphological phylogeny of spiralian with Ecdysozoa as an outgroup with a soft topological constraint that forces the monophyly of a spiralian clade that excludes chaetognaths. Phylogenies inferred under the mk + gamma model in MrBayes.

Table S1

	Bilateral chitinous jaw apparatus	Jaw cuticular membrane	Sub terminal anus	Anus position dorsal	Lateral fins	Tail fin	Cephalic hood	Ventral ganglion/ caudal ganglion	Subterminal adhesive structure
<i>Amiskwia</i>	+	+	+	?	+	+	+	?	-
<i>Inquincus</i>	+	?	+	?	-	-		?	+
Chaetognatha	+	-	+	+	+	+	+	+	-
Gnathostomulida	+	+	(+)	(+)	-	-	-	-	-
Micrognathozoa	+	+	(+)	(+)	-	-	-	-	-
Rotifera	+	+	+	+	-	-	-	+	+
Trochozoa and Rousphozoa	-	-	+/-	-	-	-	-	-	+/-

Table S1 Characters in Gnathifera, Chaetognatha, *Amiskwia* and *Inquicus*. Related to Figure 3 and Figure 4. ‘+’ indicate a presence, ‘-’ absence. ‘(+)’ refers to the intermittent opening of the gut in a dorsal and subterminal position in these taxa.